RECENT DISCOVERIES OF FOSSIL VERTEBRATES IN THE WEST INDIES AND THEIR BEARING ON THE ORIGIN OF THE ANTILLEAN FAUNA.

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Introduction. Interest of West Indian Fossils—Review of Earlier Knowledge.

Ten or twelve years ago almost nothing was known of the extinct vertebrates of the West Indies. There was good reason to suppose that a considerable fauna had existed, and that if found it would be a very interesting one. One would expect to find peculiar insular types, different from the mainland faunas, and the affinities of the various types would provide evidence as to former land connections and other interesting problems. The modern fauna of the islands has undoubtedly been greatly modified by man, both before and since its settlement by white men. Such indigenous mammals as existed have mostly disappeared in consequence, and with them many of the lower vertebrates and invertebrates. And many animals have been introduced either by intention or by accident. *Capromys, Plagiodontia* and *Solenodon,* two peculiar rodents and a very peculiar insectivore, are the only surviving mammals that are certainly indigenous. The lower vertebrates are more numerous, but many of them also have been exterminated, and others introduced since man arrived on the islands.

The climate and geology of the islands limit the prospects of discovery of fossil land faunas to cave and stream or spring deposits of Pleistocene age. The underlying sedimentary formations are practically all marine, chiefly Tertiary limestones and an older metamorphosed series which seem to be chiefly altered volcanic ma-

terial. The freshwater and littoral sediments of continental areas are unknown in the West Indies, even in the larger islands (with one or two unimportant and doubtful exceptions) and it is from these that our fossil records of land animals are almost wholly derived. There was, and is, therefore, very little prospect of discovering remains of the Tertiary or pre-Tertiary land faunas of the West Indies. The possibilities are practically limited to the Pleistocene.

Up to a few years ago two important discoveries had been made. One was the giant rodent *Amblyrhiza* found in cave-breccia on the island of Anguilla, and described by Cope in 1869. The affinities of this animal, about the size of a capybara, have been disputed, Cope regarding it as allied to the South American chinchillas, while J. A. Allen considered it as a relative of the extinct Castoroides or "giant beaver" of North America. Dr. Allen's view, although mistaken, seems to have been more generally accepted. The other discovery was a ground-sloth jaw and some other remains found near Cienfuegos in Cuba, and described by Dr. Leidy under the name of *Megalocnus,* as a near relative of the North American ground-sloth *Megalonyx.* For reasons that I shall explain later the Cuban discovery was little known and more or less discredited in scientific discussion. The *Megalocnus* was supposed to be identical with *Megalonyx,* but many doubted whether the specimen really came from Cuba. Such as it was, the evidence from fossils seemed to point strongly to a land connection with North America as late as the Pleistocene, extending at least as far as Anguilla. This no doubt played its part in the very prevalent belief in an Antillean continent, united with the greater continents to north and south of it, destroyed only in times geologically very recent.

The characters of the modern Antillean faunas were very difficult to reconcile with this hypothesis. Their insular character is very marked, whatever theories might be entertained as to the origin of the various animals. And what was known of the geology did not at all accord with the view that they were fragmented remnants of a great continent recently broken up. A diligent search for fossil remains and a more thorough and systematic study of the geology was very much needed.

The Porto Rico Discoveries.

With these and other considerations in mind, the New York Academy of Sciences decided in 1913 to undertake a systematic survey of the geology and natural history of Porto Rico, in coöperation with the local government and with the American Museum of Natural History. This was very ably conducted under direction of Dr. Britton. The geology was quite thoroughly investigated by Drs. Berkey, Reeds and others and the reports afford a better knowledge and understanding of the geologic history of this island than we have of any of the others. The marine limestone yielded one interesting fossil mammal, a sirenian or sea-cow allied not to the manatees as one would expect, but to the old-world dugongs.

The most important find in the way of land animals was made in the course of investigations in a cave near Utuado, where human remains probably prehistoric were unearthed, and beneath them remains of several kinds of extinct mammals. This stimulated further search of the numerous caves in the island, undertaken by Mr. Anthony for the American Museum of Natural History, and the results of his very successful work have been published in a well-illustrated memoir issued last December.

The fossil mammals include one insectivore, one edentate and a number of rodents, all new and very peculiar types, widely different from any known animals; also a number of bats closely allied to the living bats still on the island. Most of this fauna is represented by well-preserved skulls and various bones of the skeleton.

The insectivore *Nesophontes* is so distinct that it has to be placed in a family by itself. It has some distant affinities with the Soricoidea (moles and shrews), but is a very primitive type, and its nearest allies are perhaps to be found among the Eocene insectivora of North America. There is no suggestion of relationship to *Solenodon,* the only other known insectivore of the West Indies, nor to the extinct *Necrolestes* of South America, the only insectivore belonging to that continent. Like the Eocene insectivores it retains a great deal of the primitive tri-tubercular type of dentition which nearly all—if not all—the primitive mammals once possessed.

The edentate, *Acratocnus,* is not less interesting. The skull is superficially much like the two-toed tree sloth *Cholœpus,* with the

same type of triangular tusks and is of quite moderate size. Its nearer affinities, however, are with the great extinct ground sloths. It belongs to the same family as *Megalonyx* of the North American Pleistocene, but is not very closely related to it, and is very much smaller and in some respects more primitive. Although thus related to a North American genus of ground sloths *Acratocnus* points to a South American origin, for *Megalonyx* is known to be an immigrant type in the north, derived from South American ancestors in the Miocene.

The rodents all belong to the Hystricomorph or porcupine section of this order, which has its headquarters in South America.

The largest of them, *Elasmodontomys,* is closely related to *Amblyrhiza,* the gigantic extinct rodent of the island of Anguilla. Another smaller genus, *Heptaxodon,* also belongs in this neighborhood, but is less closely related. These are put into the family Chinchillidæ, but their nearest affinities are with the extinct *Megamys* and *Tetrastylus* of the Pliocene of Argentina.

A second group of rodents, *Heteropsomys* and *Homopsomys,* is related, but rather distantly, either to the living agouti, *Dasyprocta,* or the spiny rats of South America; it has also, as will appear, some extinct relatives in Cuba and Hayti.

A third extinct rodent from Porto Rico, *Isolobodon,* is nearly related to *Plagiodontia,* an extinct or almost extinct rodent of Hayti, and more distantly to the hutias (*Capromys*) still living in Cuba and Jamaica. Like the preceding group it is rather distantly related to any continental rodents; it is referred to the Octodontidæ.

That is the full extent of the mammal fauna of Porto Rico. Its affinities are chiefly South American, but distant, pointing to long isolation. The near relationship to the extinct Anguillan rodent is significant. The bank of shallow water which extends eastward from Porto Rico includes the Virgin Islands; and Anguilla with the adjoining islands also stands on a shallow bank of considerable extent. Vaughan has shown the probability of part or all of these banks being above water in the Pleistocene. But between the Virgin Islands and the Anguilla group there is a narrow trench of very deep water. Possibly this trench is due to faulting of recent origin and the islands were connected in the Pliocene or Pleistocene. The

alternate is to suppose that *Amblyrhiza* is a gigantic descendant of some small rodent that got drifted over the intervening sea barrier. Anguilla, it must be remembered, is but a small remnant of an island of very considerable size, as indicated by the extent of the surrounding shallow bank.

The Cuban Discoveries—Ciego Montero—Casimba—Cave Fossils. The Fauna—Insectivora—Edentata—Rodentia—Reptilia.

Ciego Montero.—The first discovery of fossil mammals in Cuba was made in 1860, in the early days of American palæontology. A lower jaw was found in a warm spring at Ciego Montero, a few miles from Cienfuegos, with other fragmentary fossils. This jaw was exhibited at the Paris Exposition in 1867, and is now, I believe, at Madrid. A drawing of it was sent to Joseph Leidy, who immediately recognized it as a relative of *Megalonyx* and named it *Megalocnus rodens* on account of the peculiar position of its tusks which simulated those of the rodents. In 1865, 1871 and 1875 De Castro published articles on extinct animals in Cuba, in which he figured this jaw and also described supposed fossil remains of *Equus* and *Hippopotamus,* and contended that these proved that Cuba had formerly been a part of the North American continent. These associates unfortunately tended to discredit the whole paper, especially the hippopotamus tusks. They did not appear to be very old, and were regarded as probably post-Columbian. The *Megalocnus* jaw was confused with the true *Megalonyx* and the suggestion was made that it was probably brought over from Central America.

Carlos de la Torre, professor of zoölogy at the University of Havana, was well aware that the *Megalocnus* had really been found in the Ciego Montero spring, and from time to time, as his duties permitted, made further investigations to see if something more could not be found at this locality or elsewhere. He succeeded in finding a few additional specimens here and better material at some other localities, and in 1910 published a notice of these discoveries. The specimens were exhibited by him at the International Congress at Stockholm and Gratz, and were deposited at the American Museum for further study and full publication in a memoir by de La

Torre and myself. The following year Mr. Barnum Brown, on Professor de La Torre's invitation and with his aid, made a more thorough exploration of the Ciego Montero spring, and secured a large collection. In 1918 Mr. Brown completed the exploration of the deposits around the spring, securing much additional material. Preliminary notices of these collections have been published, the full descriptions being postponed until all the available material had been secured. The exploration of the deposit was a rather difficult matter as the spring is a powerful one and the water had to be pumped out and drained away by means of a gasoline pump, and the spring openings cemented up, before the deposit around it could be thoroughly explored.

The Ciego Montero collections consist chiefly of bones of *Megalocnus* and *Crocodilus,* plates of a giant tortoise and a terrapin, and a few remains of other ground sloths, of rodents, lizards and birds, and a good many bones of small amphibians.

The Casimba.—Another important locality discovered by Dr. de La Torre was in the Sierra de Jatibonico, in the central part of the island, a fissure-spring at the bottom of a ravine where there was a considerable deposit with fossil bones. These correspond with the remains found at Ciego Montero, except that the smaller ground sloths were relatively more common. The material is equally well preserved, but not nearly so much of it. This locality has also been worked out.

A number of similar fissure springs were examined by Dr. de La Torre and a few fragmentary fossils secured, but nothing of importance. Probably deposits of this character may be discovered in other parts of the island, and some further discoveries may be made in this way.

Cave Deposits and Kitchen Middens.—There are also many caves in the limestone formations of Cuba, in all parts of the island. A considerable proportion of these contain guano or similar phosphatic deposits which have for many years been dug out and used for fertilizer. A few of them have recently been explored for fossils, and some very interesting material secured. The old Indian kitchen-middens, some in the caves, some elsewhere, have been more or less exploited for prehistoric human remains by the anthro-

pologists, and incidental to this work a few remains of extinct animals have been secured and described by Dr. Gerrit S. Miller, of Washington. Dr. Glover M. Allen has also published a note on some interesting cave fossils secured by Dr. Thomas Barbour. The largest cave collection yet secured was made by Mr. Barnum Brown last winter in a deposit discovered by Dr. Barbour and explored by us on his invitation.

These cave faunas consist chiefly of the remains of the small animals, rodents, insectivores, bats, etc., which are rare in the spring faunas. Remains of the ground sloths are rare, but they do occur.

Quite recently Mr. Harrington, in exploring certain caves at the far eastern end of the island for the Museum of the American Indian, secured some remains of extinct animals that warrant further search. They were chiefly *Megalocnus,* showing that this animal ranged through the whole of Cuba in the Pleistocene.

The fauna of these cave and spring deposits is a very interesting one. Fortunately the two supplement each other, so as to give a pretty full representation both of the large and of the small animals. Each consists of many hundreds of jaws, with a proportionate number of other bones. It is fair to conclude that it gives us a pretty good line on the characteristic mammals of the Cuban Pleistocene. Further discoveries may bring other animals to light, but as the same types recur in each deposit, common in one, rare in another, it does not seem likely that they will make any great additions to the fauna save through genus—and species—splitting, analogous to what has been going on among modern mammals for the last few decades. For obvious reasons it is better for palæontologists to be conservative in this respect—even at the risk of being stigmatized as "lumpers."

Insectivora.—The existing *Solenodon* has not been found fossil. This is not surprising, as it is very rare now, and may have been rare during the Pleistocene. The extinct *Nesophontes* of Porto Rico is represented in Cuba by a much smaller species distinct in various particulars. It has been described by Dr. G. M. Allen as *Nesophontes micrus.* Mr. Brown secured a great series of jaws, etc., of this species in his cave collection, but only a single jaw and a tooth at Ciego Montero.

Edentates.—The edentates are all ground sloths related to *Megalonyx,* but belong to four distinct genera. The largest and most abundant is *Megalocnus,* about the size of a black bear. The tusks are flattened into a meniscus cross-section, and set near together, especially in the lower jaw, so that it has a curiously rodent-like effect. The cheek teeth are exceptionally long, and in consequence the palate is depressed below the level of the cranium, and the jaw extremely deep. This is like the gigantic *Megatherium,* but the form of the cheek teeth is almost exactly as in *Megalonyx.* Detailed comparisons show that the Cuban genus is most nearly related throughout to *Megalonyx.*

Mesocnus is a smaller and more primitive genus, which is about the size of the Miocene ground sloths of Patagonia, and like them has a long tongue of bone projecting forward between the tusks. The cheek teeth are not so long in this genus, but they have almost the same form as in *Megalocnus* or *Megalonyx,* different from the more primitive form of the cheek teeth in all the Miocene Megalonychidæ. The tusks are rather small and not so broad or meniscoid in section as in *Megalocnus.* On the whole this is a more primitive genus, except the humerus, which has lost the entepicondylar foramen, as in *Megalonyx.*

Miocnus is of about the same size as *Mesocnus* but quite distinct. It is very closely related to *Acratocnus* of Porto Rico, perhaps the same genus. It has a short wide jaw and stout triangular tusks with a short, bony tongue between.

Microcnus is the fourth genus of ground sloths, an animal about the size of a cat, smaller than the living two-toed sloth. It resembles *Megalocnus* in the form and position of the tusks, but the molars are not so long-crowned and differ considerably in form, with a marked suggestion of the square cross-section of the Megatheriidæ. I have not seen the skull or upper teeth; a couple of foot bones doubtfully referred to this genus come nearer to the living tree-sloths in proportions than they do to any of the large ground-sloths. It would be very interesting to know more about this little animal.

There is so much individual and age variation in ground sloths that it is difficult to say how many species of these genera are pres-

ent. *Megalocnus* occurs abundantly both at Ciego Montero and the Casimba, but apparently only one species at Ciego Montero, while at the Casimba there may be two or three. The species found at the eastern end of the island agrees better with the Casimba forms than with the Ciego Montero species. Of the smaller forms there are clearly two species of *Mesocnus,* but I see no proof of more than one of *Miocnus* or *Microcnus.*

All these Cuban ground sloths, along with the Porto Rican genus, are most nearly related to *Megalonyx* among the continental genera, and may be regarded as co-descendants with it of *Eucholœops* and *Megalonychotherium* of the Patagonia Miocene. *Microcnus* is apparently the least closely related; and the relations between *Miocnus* and *Acratocnus* are very close.

Rodentia.—The fossil rodents are all hystricomorphs related to the South American rodents, but not closely related. There are two groups of them (in a broad sense) each with two or three species. One is still common on the island, the Hutias with two very closely related genera, *Capromys* and *Geocapromys*: Of these *Capromys* is common in the latest cave deposits, but in the older levels of the cave material only *Geocapromys.* The species in the older levels are all small—some are smaller than any surviving species. The large species appear only at the top. The other group is entirely extinct; it consists of three or more species apparently of a single genus which Mr. Miller has called *Boromys.* It is related to the spiny rats of South America, but not closely. *Capromys* on the other hand has a near relative in Venezuela *Procapromys.*

None of the Chinchillidæ of the eastern Antilles have been found in Cuba.

Remains of *Geocapromys* occur rarely in the Ciego Montero and Casimba collections; they are very abundant in the cave collections. *Boromys,* although common in the caves, has not been found at the Casimba or Ciego Montero. Dr. Barbour tells me that there is some reason to believe that this genus still survives in Cuba, although it has not found its way into any scientific collections.

Reptiles.—In the Ciego Montero collection is a series of fine skulls of crocodiles, which Dr. Barbour regards as all growth stages of the living Cuban crocodile *C. rhombifer.* This species has a

broad head, and in some other characters approaches the alligator. It is closely allied to the alleged Central American species *C. moreletii.*

The most interesting of the reptiles is a giant tortoise resembling in several respects the living species of the Galapagos islands. It has a very thin shell, like most of the species of oceanic islands, but aside from this, which is probably due to parallelism, it shows some other points that are suggestive of a true relationship, although not a close one. It has one or two points suggestive of relationship to the South American tortoise *T. tabulata,* but mostly differs widely from it. Comparison with the fossil tortoises of the North American Tertiary does not indicate any special relationship, although it may be regarded as a descendant of some species of this group. It has one very curious character, unique in so far as I have made comparisons, in that the margins of the horny shields are marked on the plates not by furrows but by sharp, raised crests over the greater part of the carapace. This alone would forbid any close relationship with any of the species I have compared.

Leidy named this species *Testudo cubensis* in 1868, from a broken plate of the carapace that had been sent to him.

The terrapin is probably identical with the living Cuban terrapin, which is regarded by some as a distinct species, by others as a subspecies of the yellow-bellied terrapin *Chrysemys* (or *Trachemys*) *scripta* (=*scabra*) of the southeastern states. It is at all events closely related, and belongs to a group which has several fossil representatives in the Pleistocene of Florida and other states of the southeast.

Some fragmentary remains of lizards, snakes, birds and amphibians occur in the collections, but have not yet been studied. I doubt whether very much of interest can be got from them, as they seem to be very doubtfully identifiable.

Hayti, Jamaica and the smaller islands are as yet unexplored territory. Except for the *Amblyrhiza* of Anguilla and a few fragments described by Dr. Miller from an Indian kitchen midden at S. Pedro de Macoris, in Hayti, nothing is known of their extinct fauna. Limestone caves are numerous, and will undoubtedly furnish important finds in the near future. A primitive sirenian, *Prorastomus,* was described many years ago by Richard Owen from the

older Tertiary marine limestones of Jamaica. It is distantly related to the manatees, but it throws no light upon the problems here considered, and may be passed over without discussion.

Review of the Fauna an now known. Its incomplete and insular character. Uniformity throughout the larger islands. Probable derivation of the several groups. Methods of colonization.

So much for the new discoveries. We may now review the fauna as a whole, living and extinct, and consider its general character and what bearing it has upon the past history of the islands. I shall deal principally with the mammals, partly because I am best acquainted with them, partly because the new discoveries are chiefly in this group, and partly because I think they afford the best evidence upon certain critical points.

The most obvious features to me in the mammal fauna are its incompleteness and insular character. There are no perissodactyls, no artiodactyls, no proboscidians, no carnivora, no primates, no marsupials, no rodents except three groups of the Hystricomorphs which are an especially South American group, no insectivores save for two types which have very remote affinities to any living groups, none of the various types of edentata, except a single group of ground sloths. Certainly this poverty of mammalian fauna is not to be explained by scantiness of material. We have very large collections, many hundreds of jaws and a due proportion of other bones, from two types of deposit, a cave and a spring fauna. Correspondingly large collections from cave or spring faunas in North America or South America yield very different results. Compared with the Port Kennedy, Conard Fissure or the California cave faunas, or those described by Lund and Winge from Brazil, the contrast is very striking. Spring faunas may be less varied, but whatever else is absent the larger ungulates are sure to be found in such situations.

The whole Antillean mammal fauna consists of only six types or groups of sub-family rank at most, as follows:

1. Ground sloths allied to *Megalonyx*—5 genera.
2. Rodents of the *Capromys* group—4 genera.

3. Rodents of the *Boromys* group—2–4 genera.
4. Rodents of the *Amblyrhiza* group—3 genera.
5. *Nesophontes* } two very aberrant and primitive insectivores.
6. *Solenodon* }

These six groups constitute the surely native fauna. Most of them are extinct; all of them except *Solenodon* are found as fossils. Sixteen genera and about thirty-five species.

There are various other mammals recorded as from one or another West Indian island. Some of them are known to have been introduced by man, others may have been. They are all species identical or closely related with continental species. If any of these were not introduced by man, they must have reached the islands in comparatively recent times, geologically speaking, not earlier than the Pleistocene, and some quite surely post-Columbian. Some are found fossil, indeed, but never much altered by petrifaction, in the uppermost levels of the cave and spring deposits. Such animals as the European rats, domestic cat, domestic pig, etc., belong obviously to post-Columbian time; the agoutis and armadillos of the Windward Islands and other continental American species are probably introduced by man, but they may not all be post-Columbian. Such species as the Bahaman and Martinique raccoon, the Jamaica rice rat, etc., described as distinct species, but certainly very closely related to continental species, may also have been brought by man, but long enough ago to have developed distinct races which have been accorded the rank of species. Some may indeed have come by natural means, and if so they can only have come through overseas drift, but for the present it is best to limit the discussion to the purely native groups, all of which are genera, subfamilies or families peculiar to the islands.

The first group, the ground sloths, consists of four very distinct genera allied to the Pliocene and Pleistocene North American *Megalonyx* and descended from the South American Miocene *Eucholœops.* No Megalonychidæ are found in the South American Pliocene or Pleistocene; they are replaced by more progressive and specialized families. From th eevidence one may infer that they reached the Antilles at the end of the Miocene or beginning of the Pliocene, and that the four genera specialized there in adaptation

to the insular conditions. Their peculiar specializations and the absence of any of the later and more progressive types of ground sloths that spread all over the North American continent involves isolation since that time, from North, South or Central America.

The second group, the rodents of the *Capromys* type, affords some contrast in its scope and relations. Instead of having four or five very divergent genera quite wide apart structurally, we have in the western Antilles, two closely allied genera, much closer in the skeleton than they are superficially. They are the only native mammals on the islands that are not on the verge of extinction; under natural conditions they would apparently be a very prosperous group. The cave records indicate they were rapidly progressing in size and increasing in relative numbers in the Pleistocene. And finally *Procapromys* of Venezuela, their nearest continental relative, is quite closely related. They have not had time to diverge very far from it in structure, although the record shows that they were diverging. The surface inference is that this group was a comparatively late arrival, perhaps early Pleistocene, perhaps late Pliocene, clearly much later than the ground sloths. Yet they had reached several of the western islands—Jamaica, Cuba, one of the Bahamas, even Little Swan Island, a small islet off the coast of Honduras. In Cuba several species of *Capromys* now exist. *Geocapromys* was formerly the principal or only type in Cuba, but is now found only in Jamaica, Little Swan Island and Plana Key on the Bahamas. In the eastern islands we find two genera less closely related. *Isolobodon* of Porto Rico is extinct and *Plagiodontia* of Hayti is practically extinct; these two are less closely related to the two western genera, but are regarded by Mr. Anthony as the eastern representatives of the group. Systematic exploration in the caves of Hayti would probably clear up the true relationship of these eastern genera; casual sketchy exploration or work undertaken simply to get material and describe new species, is very likely to destroy such evidence as exists on their palæontologic history.

The third group, the *Boromys* group of rodents, is extinct (possibly a single survivor) and includes a number of species belonging to two very closely related genera, doubtfully separable, one found at several points in Cuba, the other from Hayti. It is rather dis-

tantly related to the spiny rats of South America (*Echinomys*). *Heteropsomys* of Porto Rico is rather doubtfully related to this group; certainly the affinities are distant. Jamaica is unknown palæontologically.

The fourth group, the rodents of the *Amblyrhiza* group, is limited to Porto Rico and Anguilla, that is to say, to the eastern end of the east-west chain, and is wholly extinct. *Amblyrhiza,* the largest, is quite gigantic for a rodent, about the size of the Capybara or of the extinct *Castoroides. Elasmodontomys* of Porto Rico is nearly the size of a beaver. *Heptaxodon* of Porto Rico is a smaller form. These West Indian chinchillids are only distantly related to the living Chinchillidæ of South America, but they are quite nearly related to the *Megamys* group of the South American Pliocene.

The fifth and sixth groups of mammals, the two insectivora, are the most isolated of all the West Indian mammals, each having a family to itself. They are not at all related to each other, and their nearest relatives appear to be certain imperfectly known Eocene and Lower Oligocene genera of North America. There are no autochthonous insectivores at all in South America, save for the curious little *Necrolestes* of the Miocene, which may have had something to do with the Chrysochloridæ, but certainly not with these West Indian genera. On the other hand, insectivora occur in all the Tertiary formations of North America, and were more abundant and varied in the older Tertiaries. *Micropternodus,* of the Lower Oligocene, may have been a distant ancestor of *Solenodon,* and several of the Eocene soricoid genera from the Bridger show much resemblance to *Nesophontes.* But any exact relationship is to be regarded as provisional, and by no means proven.

Turning now to the reptiles, we find that the entire order of chelonia is represented to-day by a single species of terrapin widely distributed through the islands, found fossil in Cuba, possibly also in the island Sombrero, and closely related to the yellow-bellied terrapin of the United States. It belongs to a North American group, its nearest fossil relatives are in the southeastern states, and the few terrapins of Central and South America, which are probably rather late immigrants from North America, are less closely

related to the West Indian species. All this points strongly to Florida as the source, and the Pleistocene as the time of arrival.

A giant tortoise, new extinct, is found in Cuba. Unlike the terrapin, it is only distantly related to any other tortoises, somewhat nearer to the species of the Galapagos islands than any other. It does not appear to be especially related to any North American tortoises, except that it may be descended from some primitive species of the Miocene. True tortoises are found in the Pliocene and Pleistocene of South America, but are believed to be immigrants from the north. The Galapagos islands affinities suggest that this species may be derived from the unknown Tertiary fauna of Central America. But the Cuban species must have been isolated a long time, at least since the beginning of the Pliocene, one would judge from its peculiar specialization.

The crocodiles of the West Indies are two, one, *C. rhombifer,* peculiar to Cuba. The fossil species in Cuba is *C. rhombifer,* a broad-headed alligator-like form. It is said to be nearly related to the alleged *C. moreletii* of Central America. The other species, *C. americanus,* is found in Florida, Mexico, Central America and the west coast of South America as far as Ecuador, and appears to be rather widely distributed in the West Indies. It is probably significant that this widely distributed species inhabits the salt marshes, whereas the more local *C. rhombifer* occurs in fresh water.

The smaller reptiles and amphibians, fresh water fish, and the various groups of invertebrates are much more widely distributed throughout the West Indies. Their distribution and its causes have been extensively discussed by various authors, but unfortunately without giving due weight to two features in which it differs from the mammals and the two groups of large reptiles.

First that the dispersal of these lower groups on oceanic islands is probably chiefly brought about by storms. The eggs, attached to small débris, or even the adult animals, if small enough, will often be picked up by violent storms, and carried for considerable distances. A cyclonic storm or tornado will sometimes partly empty a shallow pond, carrying the materials a mile or more into the air, the lighter and smaller débris being carried along for a great many miles before it comes to the ground again. On account again of

their small size they would not be crushed by the fall. The distribution of the infra-mammalian groups in the West Indies, as on all other oceanic islands, appears to me to be much more in accord with this method of transportation than with any continental bridge theories or current borne drift. Mammals, however, could hardly be successfully colonized in this way, nor would it serve for chelonians or alligators. But it does probably apply to most birds and nearly all bats.

The second feature in regard to the infra-mammalian groups is that we know little or nothing of their past distribution. From such slight direct evidence as we have, and from the analogies of past distribution of the mammals, we can be reasonably sure that it was not the same in the later Tertiary as it is now, and on the same evidence I am confident that the methods of inferring past from present distribution generally used by zoögeographers are erroneous. If applied to mammals such methods would lead to conclusions absurdly in conflict with the known facts; they are in conflict with the few available data among the lower land animals; and they appear to me to be based upon erroneous theoretical reasoning.

Summarizing the data briefly we have among the mammals:

1. The ground sloths, probably of South American origin (but possibly via Central America) which must have arrived about the late Miocene or early Pliocene, and demand isolation since that date to account for their diversity, archaic type, and absence of later developed and more progressive relatives.

2. The rodents, all Hystricomorphs broadly of South American affinities, but including three groups.

(*a*) Chinchillids, limited to the eastern islands, and most diverse and peculiar. They also have come from South America, but from the eastward, in the late Miocene or Pliocene.

(*b*) Hutias, including an eastern and a western group (but the division line is not the same as with the chinchillids), the western group with one near relative in Venezuela, the eastern genera (Hayti and Porto Rico) more isolated. I have formulated several different hypotheses to account for the distribution, but none can be sufficiently tested by facts to be of much account. The clue lies, I think, in a knowledge of the Pliocene and Pleistocene fauna of Cen-

tral America, but the eastern representatives may have come from South America independently at an earlier date. Too few data to go upon. (See addendum, p. 181.)

(*c*) The *Boromys* group, known as yet very imperfectly, apparently limited to Cuba and Hayti. These also are quite distant from any continental forms, suggesting their having been isolated since the Pliocene, but so far as we know this is not supported by diversity of genera or insular specializations as among the ground sloths. The relationship to this group of the Porto Rican *Heteropsomys* is in dispute, and it is well to defer conclusions.

3. The insectivora are much more isolated than any of the preceding, but their relations are, although remotely, North American. It is with the early Tertiary fauna of North America that their apparent affinities lie.

4. The giant tortoise has distant relations with the species of the Galapagos islands, but has evidently been isolated and insular for a long time, since the Miocene or early Pliocene, but not earlier than that. The terrapin, on the other hand, is quite closely related to a living species of the southeastern states and to a group of Pleistocene species in the same region. It can hardly be supposed to be older on the islands than the Pleistocene, especially since the several islands in which it is found have not developed even distinct subspecies, although there is a good deal of individual variation.

5. The Cuban crocodile is common in the Pleistocene and probably reached the island somewhat earlier; it is nearly related to a Central American species, but it is quite as likely as not that that species was more widespread in the Pliocene, perhaps through the Southern States. (See addendum, p. 181.)

6. Birds, bats, lizards, snakes, amphibians and fresh water fishes, molluscs; insects and various other groups of invertebrates are more widespread on the islands, as they are generally on oceanic islands. I do not think the reason is so much their greater geologic age as it is their greater facilities for dispersal, especially through storms, as I have indicated. Generally speaking there are in each group forms allied closely to modern mainland forms and others which are more isolated, primitive and archaic in type, usually more

sedentary in habit or otherwise unfavorably situated for dispersal. Time is lacking to discuss these further.

Two questions are involved in the interpretation of this fauna. First as to former connections between the islands themselves, second as to former connections with the mainland.

There is considerable to be said in favor of Pleistocene or late Pliocene connections between the greater Antilles, extending as far east as the Anguilla group. In favor of this are the presence of representative species or genera of mammals as follows:

Nesophontes on Cuba and Porto Rico.

Solenodon on Cuba and Hayti.

Miocnus on Cuba and the closely allied *Acratocnus* on Porto Rico.

Boromys and *Brotomys* on Cuba and Hayti.

Capromys and *Geocapromys* on Cuba, Jamaica and one island of the Bahamas, also on Little Swan Island.

Isolobodon and Plagiodontia on Porto Rico and Hayti.

Amblyrhiza on Anguilla and *Elasmodontomys* on Porto Rico.

Against such connections are to be cited

(1) The absence of three out of the four ground sloth types from Porto Rico.

(2) Limitation of the *Capromys* group proper to the western islands, of the chinchillids to the eastern islands.

(3) Representative or replacing types are in some cases closely, in others much more distantly related as between the various islands of the chain. No specific sequence of geographic separation can be formulated that will fit the known facts. In some cases it would call for an earlier separation between Cuba and Hayti, in others between Hayti and Porto Rico.

On the whole I feel that this question is better left open till we get more data, especially as to the fossil faunas of Hayti and Jamaica.

As to the second question, of continental connections, it seems to me that the weight of evidence is very heavily against it. There are two broad considerations affecting the matter. *First,* the geologic evidence and the submarine topography, while they do not forbid certain former connections, are on the whole unfavorable to

any. The islands are not the remnants of a former Antillean continent; on the contrary they have been built up, partly by uplifting and uptilting of blocks along fault-lines, partly through volcanic eruptions, largely submarine, along the lines of weakness and faulting. They are not very old geologically, the oldest known rock being the marine Jurassic of western Cuba; nearly all if not all of the metamorphic rocks mapped by the U. S. Geological Survey as Palæozoic are either certainly or probably Cretaceous; and the lesser Antilles are the youngest geologically. A land connection with Florida is practically forbidden by the geology; a land connection via the lesser Antilles is unlikely in the later Tertiary, and very unlikely earlier; a land connection via Hayti, Jamaica and Honduras is unobjectionable, but there is no particular evidence in the geology or submarine topography to show that there *was* such a connection in the Tertiary. There is, however, considerable to indicate that the relatively shallow banks that stretch eastward from Honduras and Nicaragua almost to Jamaica may have been partly or wholly out of water about the Pliocene or Pleistocene. In short, if a continental connection is required by the faunal evidence, this is by all odds the most likely place for it.

The *second* general consideration is the incomplete character of the fauna. It is not a continental fauna, either North or South American, but an insular fauna arisen from development in isolation of a few individual elements of each. Such a fauna is not the result of invasion from North or from South America over a continuous land area. Its incompleteness can no longer be ascribed to extermination by man, for we see that the Pleistocene fauna, while much more extensive, was obviously and significantly incomplete and insular in type. It cannot be ascribed to scanty fossil material, for we have now very large collections of both cave and spring fossils. It cannot be ascribed to drowning out of the fauna, for we have surviving on the islands two types of Insectivora that date back to the middle or early Tertiary.

A more particular examination of the different groups of mammals, etc., confirms this general conclusion. The several groups indicate derivation from different sources geographically, and at different times geologically. If we insist upon the need of conti-

nental bridges to account for the West Indian mammals, it is not one but several bridges that they would indicate, each lasting only long enough to permit the passage of one or two of the least migratory elements of the continental faunas, and the later ones so arranged as not to disturb the isolation of the types which had already reached the islands. If continental connections be demanded, the chinchillids call for a Pliocene bridge via the lesser Antilles, not extending west of Porto Rico. The *Capromys* group calls for a Central American bridge in the late Pliocene or Pleistocene, while the ground sloths would demand a Central American bridge in the late Miocene or early Pliocene and subsequent isolation. The giant tortoises similarly would call for connection with the Galapagos islands and isolation since Miocene or early Pliocene, while the terrapin demands a Pleistocene bridge with Florida impassable for everything but one terrapin. The two insectivora similarly would call for an Oligocene connection with North America and subsequent isolation. Such conclusions seem to me inconsistent and improbable.

I do not think that one should trust blindly in these indications of former geographic relations from faunal affinities. But I do think that so far as they are of value, they should be fully and fairly presented. It will not do to pick certain points that may fit in with a particular theory, and gloss over or ignore discrepancies; nor do I see much profit in inventing elaborate hypotheses depending upon a series of unknown factors or unprovable assumptions to account for discrepancies. One may of course say that we do not know what the Tertiary fauna of Central America was like, and that it may have contained just the necessary elements to account for the West Indian fauna through a Pliocene connection. But that merely transfers the difficulties that confront one in attempting to work out any solution that conforms with all the faunal indications. It shifts the problem from the West Indies to Central America. It does not solve it.

The only explanation that seems to me conformant with all the data, physiographic, geologic and faunal, is that the islands have been populated by colonization through storms and ocean drift without land connection with the continents, but aided by extension of

the land areas to or near the borders of the continental shelf in the Pliocene and Pleistocene, and perhaps by some further connections between the greater Antilles. The mammals and chelonians would seem to be practically limited to ocean drift as a method of transportation. I have elsewhere discussed the probabilities of this method in its relation to the length of geologic time; and may add here only that if the estimates made by Barrell of the length of geologic periods are accepted, the chances become from twenty to one hundred times more favorable. For birds and bats, the smaller egg-laying vertebrates, invertebrates and plants, the agency of storms appears to afford the simplest explanation, although wave-borne drift has also doubtless played a part.

ADDENDUM.

Dr. Barbour's admirable memoir on the Herpetology of Cuba was published too late to incorporate in the foregoing discussion the very satisfactory solution which he supplies of the alleged Central American species *Crocodilus moreletii.* He shows that this is an error of record, the species being based upon a specimen of *C. rhombifer* from Cuba. The Cuban species is therefore an isolated one in the genus, with no near continental relatives. A study of the series of fossil skulls from Ciego Montero has been undertaken by Dr. C. C. Mook, and will be published later.

Mr. Anthony has suggested in conversation with the writer that the Venezuelan *"Procapromys"* may like *Crocodilus moreletii* be an error of record, based upon a specimen erroneously credited to Venezuela, but actually coming from one of the West Indian islands and identical with *Geocapromys* or *Capromys.* This, if verified, would clear up the affinities of the *Capromys* group conformably with the distributional relations of the other rodents, solving a very perplexing problem.